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CYCLE IN THE LIFE OF THE INDIVIDUAL (ONTO-  
GENY) AND IN THE EVOLUTION OF ITS  
OWN GROUP (PHYLOGENY).\*

BY ALPHEUS HYATT.

Presented October 14, 1896.

THE organic cycle, as generally understood both by laymen and scientists, and as usually described in literature, is, as a rule, considered from a physiological rather than a structural point of view. The development of the young, and the attainment of the adult or comparatively permanent stage, complete the progressive stages. Old age, accompanied by losses of characteristics and functions and consequent weakening of the body, is retrogressive, and brings on second childhood, thus completing the cycle in the ontogeny.

My purpose to-night is to show that the cycle is also represented in the life history of the individual by definite structural changes, and that these have direct correlations with the history of the changes in the forms of the group while evolving in time.†

The fundamental discoveries that are more than any other directly useful in the study of the phenomena of the cycle, both in ontogeny and phylogeny, may be briefly noticed as follows.

The opinion that the higher animals are complex colonial aggregates of cells, which in structure are equivalents to the lowest and minutest adult forms of the animal kingdom, the unicellular bodies of Protozoa,

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\* This paper was in part read before the Academy as a general summary of the phenomena of cycles, but does not assume to be an exhaustive or even complete account of the literature or theoretical views treated of.

† These correlations have been more fully stated in a number of publications by the author, especially "Genesis of the Arietidæ," Smithsonian Contribution 673, and Mem. Mus. Comp. Zoölogy, Vol. XVI.; "Bioplastology and the Related Branches of Scientific Research," Proc. Bost. Soc. Nat. Hist., Vol. XXVI.; and "Phylogeny of an Acquired Characteristic," Proc. Am. Phil. Soc., Vol. XXXII. No. 143.

has been steadily gaining in probability since it was first announced by Oken in 1805, in "Die Zeugung," Frankfurt bei Wesche, 8vo.\* This work we have not yet seen, but in the first edition of the "Naturphilosophie," Jena, 1809, II., XII. Buch, Zoogenie, he describes protoplasm as 'Punctsubstanz' and as giving rise to the 'Blasenform oder Zellform' in both animals and plants. Oken considered the lower animals "Polypen, Medusen, Beroen, kurz alle Gallerthiere," to be composed of 'Punctsubstanz.' The nerves, the cartilage, and bones of higher animals were considered as modifications of this form of 'protoplasm,' but the skin and fleshy parts, including the viscera, were described as cellular, "dem Fleisch liegt die Bläschenform zur Grunde"; again, on p. 30, "die Eingeweide, welche am meistens aus Zellengewebe bestehen." Oken, in XII., VIII. Buch, treats of the subject we are more immediately interested with, and writes as follows: "Pflanzen und Thiere können nur Metamorphosen von Infusorien sein, . . . im kleinsten sind sie nur infusoriale Bläschen die durch verschiedene Combinationen sich verschiedene Gestalten und zu höheren Organismen aufwachsen," and also adds, on p. 29, in anticipation of one of the points advanced by the author in his "Larval Theory of the Origin of Cellular Tissues," † "auch besteht der Samen aller Thiere aus Infusorien."

This author directly compares his cystic or intestinal animals, Infusoria, with ova, and speaks of them as oözoa, and in the preface to the English edition of his Physiophilosophy, London, 1847, Ray Society, he writes that all organic beings originate from and consist of vesicles or cells. "Their production is nothing else than a regular agglomeration of Infusoria; *not, of course, of species previously elaborated or perfect, but of mucous vesicles or points in general which first form themselves by their union or combination* into particular species." Oken's view was based on the resemblances existing between the Protozoa and the cells in the tissues

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\* Through the kindness of Prof. George Baur I have received his copy of this book, and find to my surprise that it contains quite different statements of Oken's theory from that of the "Naturphilosophie." This author made great advances in knowledge between 1805 and 1809. In "Die Zeugung" he relies for the proof that the more complex animals are descended from what we now call unicellular organisms upon the constant presence of some of these in decaying flesh, assuming that they are the disintegrated elements of the body itself and not independent productions.

He makes also, on p. 128, distinct statements asserting the parallelism of the development of the individual to the evolution of the organic kingdom, but gives only fanciful analyses in support of this position.

† Proc. of the Bost. Soc. Nat. Hist., Vol. XXIII., March 5, 1884.

of the Metazoa ; and it is evident he is entitled to be considered the first teacher of the unicellular doctrine, an honor now universally given to Von Siebold.

However imperfect and imaginative the results as compared with the more objective statements of later observers, the author who wrote such sentences as these had as clear ideas as the knowledge of his time permitted, and was the Haeckel of the early part of this century, and, like him, a great and successful leader, making many errors but also many discoveries and "blazing out" some of the paths that we are still following.

Meckel\* seems to have been the first author who brought together and stated in a clear way the scattered observations and ideas with regard to the correlations existing between the transient stages of development of the individual and the so-called permanent modifications represented by the similar characters in the adult stages of similar forms.

Meckel says : "Es giebt keinen guten Physiologen, den nicht die Bemerkung frappirt hätte, dass die ursprüngliche Form aller Organismen eine und dieselbe ist, und dass aus dieser einen Form sich alle, die niedrigsten, wie die höchsten, so entwickeln, dass diese die permanenten Formen der ersten nur als vorübergehende Perioden durchlaufen. Aristotles, Haller, Harvey, Kiemeier, Autenrieth, und mehrere andere haben diese Bemerkung, entweder im Vorübergehen gemacht, oder, besonders die letzten, hervorgehoben und für die Physiologie ewig denkwürdige Resultate daraus abgeleitet.†

"Von diesen niedrigsten Wirbelthieren an bis zu den höchsten Geschlechtern lässt sich die Vergleichung zwischen dem Embryo der höhern Thiere und den niedern im vollkommenen Zustande vollständiger und treffender durchführen.

"In der That giebt es ja eine Periode wo der Embryo des höchsten Thieres, wie schon Aristotles sagt, nur die Gestalt einer Made hat, wo er ohne äussere und innere Organisation, bloss ein kaum geformtes Klümpchen von Polypensubstanz ist. Ungeachtet des Hervortretens von Organen bleibt es doch nach, wegen des gänzlichen Mangels eines innern Knochengerüsts, eine zeitlang Wurm und Mollusk, und tritt

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\* Meckel, "Entw. e. Darstellung d. zw. d. Embryonalzustände d. höhern Thiere u. d. perman. d. niedern stattfindenden Parallele." Beitr. z. vergleich. Anat., II., Leipzig, 1811, pp. 1-148. Meckel speaks of his publications as only preparatory to more extended researches.

† I desire to express my indebtedness to Miss M. F. Slack, Librarian of Mus. Comp. Zoölogy, for her assistance in finding this important reference.

erst später in die Reihe der Wirbelthiere, wenn gleich Spuren der Wirbelsäule schon in den frühesten Perioden seinen Anspruch auf diese Stelle in der Reihe der Thiere beglaubigten."

It is very obvious, from these statements of Meckel, that the correlation of embryology and the epembryonic stages of the individual with the permanent modifications of animals of simpler construction was understood, as far as was possible with existing knowledge, from the time of Aristotle, and that it was to a greater or less extent a working hypothesis at that time, and, as declared by him, had been helpful in giving a clearer understanding of the development of the individual and of the relations of the individual to the whole animal kingdom.

The next step was taken by Von Baer, in dividing the animal kingdom into four types and in limiting this general statement to animals occurring within each of these types. He also considered it highly probable (not barely possible, as it is quoted by some writers) that the earliest stages of the embryo resemble in aspect the adult stages of the lowest grade of forms in the animal kingdom. He had in mind in this statement the modern view of the affinities of the earliest stages of the embryo or its repetitions of the characteristics of Protozoa,\* so far as the knowledge of his time permitted.

Von Baer endeavored to prove that each of the four types had similar embryos, and that the type characters were determinable at early stages in the ontogeny. Both Von Baer and Louis Agassiz were pupils of Ignatius Döllinger, an embryologist who published nothing. Both of these eminent men have recognized him as their master in embryology, but have given no definite statement of what they were taught by him. Louis Agassiz accepted Von Baer's opinions, and subsequently enlarged them, when he published his work on fossil fishes, by the introduction of the element of succession in time, and thus laid the basis for all more recent investigations.

Agassiz gave the fullest expression of his views in "Twelve Lectures on Comparative Embryology," Lowell Institute, Boston, 1848-49, subsequently published in pamphlet form. One wonders, as he reads, how any man holding such views could have held his mind closed to the conclusion that animals were evolved from simpler or more primitive forms. The effect of theoretical preconceptions in closing the mind to the reception of new ideas never had a stronger illustration. Louis Agassiz, in 1849, had all the facts essential for building up an hypothesis of evolution that

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\* Entwicklung. d. Thiere, Scholion V. pp. 119, 120, etc.

would have placed him in the history of science on the same line with Lamarck and Darwin.

He states in fourth lecture, p. 26, as follows : "The results thus far obtained in the lectures which I have delivered can be expressed as follows. There is a gradation of type in the class of Echinoderms, and indeed in every class of the animal kingdom, which, in its general outlines, can be satisfactorily ascertained by anatomical investigation ; but it is possible to arrive at a more precise illustration of this gradation by embryological data. The gradation of structure in the animal kingdom does not only agree with the general outlines of the embryonic changes. The most special comparison of these metamorphoses with full-grown animals of the same type leads to the fullest agreement between both, and hence to the establishment of a more definite progressive series than can be obtained by the investigation of the internal structure. These phases of the individual development are the new foundations upon which I intend to rebuild the system of zoölogy. These metamorphoses correspond, indeed, in a double sense, to the natural series established in the animal kingdom : first, by the correspondence of the external forms, and secondly, by the successive changes of structure, so that we are here guided by the double evidence upon which the progress in zoölogy has, up to this time, generally been based.

"Their natural series again correspond with the order of succession of animals in former geological ages, so that it is equally as true to say that the oldest animals of any class correspond to their lower types in the present day as to institute a comparison with the embryonic changes, and to say that the most ancient animals correspond with the earlier stages of growth of the types which live in the present period. In whatever point of view we consider the animal kingdom, we find its natural series agree with each other ; its embryonic phases of growth correspond to its order of succession in time, and its structural gradation, both to the embryonic development and the geological succession, corresponds to its structure ; and if the investigations had been sufficiently matured upon this point, I might add that all these series agree also in a general way with the geographical distribution of animals upon the surface of our globe, but this is a point upon which I am not yet prepared to give full and satisfactory evidence. So much for the views referring to embryology in its bearing upon zoölogical classification."

And again on page 27 : —

"However, another step had to be made to show a real agreement between the earlier types of animals and the gradual development of the

animal kingdom, which has been the last progress in our science of fossils, namely, to show that these earlier types are embryonic in their character; that is to say, that they are not only lower in their structure when compared with the animals now living upon the surface of our globe, but that they actually correspond to the changes which embryos of the same classes undergo during their growth. This was first discovered among fishes, which I have shown to present, in their earlier types, characters which agree in many respects with the changes which young fishes undergo within the egg. Without entering into all the details of these researches, I will conclude by saying it can now be generally maintained that earlier animals correspond not only to lower types of their respective classes, but that their chief peculiarities have reference to the modifications which are successively introduced during the embryonic life of their corresponding representatives in the present creation. To carry out these results in detail must now be, for years to come, the task of paleontological investigations.\*

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\* Prof. George Baur of Chicago University has, since the above was written, called my attention to Carl Vogt's "Embryologie des Salmones," published under the general title of "Poissons d'Eau Douce," par L. Agassiz, Neuchatel, 1842. I take the following quotations from his pages.

Vogt says, on the second page of the Preface, after stating that Louis Agassiz had handed this part of the work over to him: "En me confiant une tâche aussi honorable, mon célèbre ami n'est cependant point resté étranger à mes recherches. Nous avons discuté ensemble les faits capitaux, à mesure que l'observation me les révélait; souvent même nous les avons examinés de nouveau en commun, et lorsque j'eus rédigé mon travail, c'est encore lui qui a bien voulu le revoir."

Again, on pages 256, 257: —

"Depuis longtemps on a discuté dans des sens très-divers la question de l'analogie entre les phases du développement des animaux vivants maintenant et les changements qui sont survenus dans l'ordre de succession des espèces fossiles; mais faute de renseignements précis sur l'un ou l'autre des côtés de la question, ces généralisations sont restées dans un vague très-fâcheux pour les vrais progrès de la science. Sans entrer ici dans des considérations hasardées, sans aborder le domaine encore trop peu cultivé de la plus grande analogie qu'offrent entre elles les différentes parties du corps des poissons fossiles les plus anciens et que l'on pourrait paralléliser avec l'homogénéité des tissus primitifs de l'embryon, je me bornerai à faire ressortir quelques points qui ne sauraient plus être contestés et qui, je l'espère, feront faire de nouvelles recherches sur l'ensemble de la question."

Vogt concludes, on page 260, as follows: —

"On pourra donc dire à l'avenir, en restant rigoureusement dans les limites de l'observation, qu'à certains égards, les espèces fossiles d'une classe parcourent dans leur succession historique des métamorphoses semblables à celle que subissent les embryons en se développant; ou vice-versa, que les embryons des animaux de notre époque passent, dans les différentes époques de leur développement par des

Perhaps in consequence of pressure of other work or of his theoretical views, Louis Agassiz seemed to have lost sight of the great importance of continuing his researches upon the meaning and correlations of the epembryonic stages. These were referred to in his publications, but were not made as prominent as they deserved after the lectures at the Lowell Institute in 1849, and in his personal talks with his students or

états analogues à ceux que présentent les espèces fossiles dans leur succession; ou en d'autres termes enfin, que le développement d'une classe dans l'histoire de la terre offre, à divers égards la plus grande analogie avec le développement d'un individu aux différentes époques de sa vie. La démonstration de cette vérité est un des plus beaux résultats de la paléontologie moderne."

These quotations antedate Louis Agassiz's direct statements since in his "Discours sur la Succession et le Développement des Êtres organisés à la Surface du Globe Terrestre," etc., Neuchatel, 1841, he does not give any embryological laws. It is of course quite possible that he did not consider it necessary to mention these in his "Discours," which, notwithstanding its title, was merely a general statement of the paleontological evidences of a plan in nature, and ended with an argument for the existence of an intelligent creator. Whether this was an omission, or that he did not at that time recognize the importance of the law of palingenesis, does not appear from the text of his publications. The first definite statement under Louis Agassiz's own hand appears to be in his "Recherches sur les Poissons Fossiles," Neuchatel, 1833-43, Vol. I. Chap. IV. p. 93:—

"J'aurai par conséquent souvent recours à l'embryologie d'une part pour rechercher les analogies entre le squelette des embryons et celui des poissons cartilagineux par rapport aux poissons osseux; d'autre part pour éclaircir les rapports qui existent entre les formes primitives que nous trouvons chez les poissons des anciennes couches de la terre, et celles qui se voient dans les premiers temps de la formation de l'embryon."

This was certainly written subsequently to the "Poissons d'Eau Douce," since Agassiz quotes Vogt upon the following pages 94, 95. He also speaks of the same on page 169, referring both to zoological rank and occurrence in time.

These are extracts from the Introduction, which was probably written and published in 1843, judging by the immediately following Preface to the first volume, which is dated 1843.

Vogt's candid admission in his Preface of constant consultations with his master, and his failure to state this law as his own discovery or to claim the authorship subsequently, lead one to think that it might not have originated with him.

Vogt fully understood the meaning and application of this law, and restates it clearly in his "Zoologische Briefe," Frankfurt am Main, 1851, p. 16, and also in his "Lehrbuch der Geologie und Petrefactenkunde," 1854, Vol. I. p. 471, and tries to apply it to the classification of different groups of the animal kingdom and to the history of their fossil remains in "Paleontologische Entwicklung," pp. 423-541. He seems to have been the first to have seen its true meaning as a law of evolution, since he completely rejects the doctrine of special creations. It may be that the only way out of this difficulty is to call this Agassiz and Vogt's law, just as it is now not infrequent to speak of Darwin's and Wallace's laws of natural selection.



in his lectures I cannot remember that they were ever treated directly by anything more than incidental references, although embryology was very often the principal theme.

Nevertheless, I must have got directly from him, subsequently to 1858, the principles of this branch of research, and through this and the abundant materials furnished by the collections he had purchased and placed so freely at my disposal, I soon began to find that the correlations of the epembryonic stages and their use in studying the natural affinities of animals were practically an infinite field for work and discovery.

Although within a year after the beginning of my life as a student under Louis Agassiz I had become an evolutionist, this theoretical change of position altered in no essential way the conceptions I had at first received from him, nor the use we both made of them in classifying and arranging forms. This experience demonstrated to my mind the absurdity of disputing the claims of any author to the discovery of a series of facts and their correlations because of his misinterpretation of their more remote relations or general meaning. It is of some importance to notice this, because it is the rule now to attribute Von Baer's and his predecessors' and Louis Agassiz's discoveries in this line to Haeckel. This eminent author has, indeed, given one of the most modern definitions of this law, and has named it the 'law of biogenesis.' Haeckel's discoveries in embryology are sufficiently great without swelling the list with false entries, but it will probably be a long time before naturalists realize and acknowledge this error. Some of the most eminent embryologists in this country have adopted the Haeckelian nomenclature without sufficient critical examination of the term under discussion. The so called Haeckelian 'law of biogenesis' is really Agassiz's law of embryological recapitulation restated in the terms of evolution.

It has surprised me that serious objections to the use of the word 'biogenesis' in this connection have not been made. This word has been long employed in another sense, as antithetical to 'abiogenesis.' The latter has been for many years applied to the theory of the generation of living from inorganic matter, and the former to the theory asserting that living matter can originate only from living matter; the use of the phrase 'the law of biogenesis' is consequently inappropriate, since neither did Agassiz's nor Haeckel's discoveries cover so much ground. The former gave us a law for the correlations of the earlier stages of ontogeny with phylogeny. This cannot be called 'the law of biogenesis,' since that has been long ago stated as the law of the origin and continuity of organism, or, in other words, the genesis and continuity of

life from and through living matter only. There are two different manifestations of Agassiz's law, which Haeckel defined and named 'palingenesis' and 'cœnogenesis,' the former referring to the ordinary or regular mode in which the characteristics of ancestors are repeated in the development of the individual, and the other to what is frequently called the abbreviated mode, etc.

These two modes are by no means all, but at present only the first or simplest manifestations of the phenomena need be treated of. This, or what Haeckel very appropriately calls 'palingenesis,' was what Louis Agassiz had studied, and, so far as all the essential facts were concerned, thoroughly understood, and it was this that he taught his students, so that it became, at any rate in my own case, the foundation of all my subsequent work in determining the mutual relations of forms. If then, as I have proposed in former publications, the term 'law of palingenesis' be adopted, this expressly states just what Louis Agassiz discovered.

Observations upon this ground made especially upon Cephalopoda have led to the discovery of correlations between the latter or epembryonic stages and the adult stages of extinct ancestors, which have greatly enlarged the field of application of Agassiz's law of palingenesis, and given it an exactitude that has made it of surpassing importance in the study of evolution. Beecher has been able to point out the single species of Brachiopod from which the whole of the vast number of distinct forms of this great group have originated. He has established this fact not only by showing that the young of the existing and fossil forms all repeat more or less at one stage the form of the adult of the initial species, but has also found a very near affine of this single ancestral species as a fossil appearing in one of the earliest of fossil-bearing formations.

Dr. R. T. Jackson has done the same work for the Aviculoids among the Pelecypoda, tracing all to one genus, *Nucula*, and has treated the Echinoidea in the same way, tracing them by the use of Agassiz's law to the genus *Bothriocidaris*.

Although the evidence is perhaps less conclusive with reference to the ancestor of Cephalopoda as a whole, this class has furnished the means of showing the action of this law in smaller groups with great accuracy. It has been possible to trace the origin of a number of smaller groups to single ancestors within the class by carefully studying the correlations of the epembryonic stages with the adults of the same group that have preceded them in time, and this study has also led to further discoveries. It has been found that the new characters were first introduced in the later stages of ontogeny, usually in the full-grown stage; then, as old age

approached, certain losses of the characters of the adult took place, or, if additional growths were acquired, these were of a peculiar kind. These senile stages had been noticed by D'Orbigny and Quenstedt, but these authors did not attempt to show that any correlations existed between any stages of the ontogeny and the gradations occurring in the full-grown forms during their evolution in time, or what is called phylogeny. The oldest stage of the shell in Cephalopoda, Brachiopoda, and Pelecypoda is commonly marked by a series of retrogressive changes, which have been fully described elsewhere. These changes have a similar nature to those found in the old age of man, but they are more noticeable because they are recorded in the permanent characters of the hardened shell. The old man returns to second childhood in mind and body, and the shell of the cephalopod has in old age, however distinct and highly ornamented the adult, very close resemblance to its own young. This resemblance is a matter of form and aspect only, since there can be no close comparison in minute structure, nor functions between organs and parts, at these two different ends of life. Such analogies, however, have their own meaning, and are of great importance when properly translated.

In the first place they show that the cycle of life as manifested in man is found also in the ontogeny of other animals and more perfectly in proportion to the perfection of the record. They are consequently among shell-bearing animals, especially those that carry their embryonic shells and all their subsequent stages of development throughout their lives, more perfect, more decisive, as well as more obvious, than in animals, like the Vertebrata, which carry no such burden of hard dead parts, upon and in which their stages of development are recorded. The cycle of the ontogeny is, therefore, not only physiological, but it is also a definite series of structural changes and is often accompanied by transformations of remarkable and sometimes startling character.

These retrogressive transformations in old age of the shells of Cephalopoda, Brachiopoda, and Pelecypoda have been found to have decided correlations with the adult characters of species that appear simultaneously or later in time. If one traces any group through its evolution in time, it has, as stated by many authors, a period of rise called the epacme, a second period of greatest expansion in numbers of forms and species called the acme, and then usually a movement towards contraction called the paracme. All three of these terms were first proposed by Haeckel, who used them largely in a physiological or dynamical sense. The epacme of any group, large or small, is usually a process of evolu-

tion by addition of new structures or characteristics based on older structures and thus leading to greater and greater complication of the primitive organization. The acme represents the time of greatest complication in structure and greatest expansion in numbers of forms for any group, large or small. The paracme is the decline, and this takes place through the reduction and actual loss of structures and characteristics that have been built up by evolution during the epacme. This is no ideal picture, but a simple statement of the experiences of those paleontologists who have patiently traced the history of groups through geologic time. Agassiz's law enables one to follow the epacme of the evolution of a species, or genus, or order, or larger group, but further correlations between the cycle of individual life and those in the evolution of its own genetic group must be sought in the correlations existing between the older retrogressive stages of the ontogeny and the paracme of each group.

The importance and peculiar nature of these correlations led me, in one of my papers, to introduce, for this branch of research, the term 'Bioplastology,' which will be found convenient by those interested in this class of work.

The following table of terms is useful here to explain the relations of the cycle of development in the individual to that of the group to which it belongs.

TERMS OF BIOPLASTOLOGY EXPLAINING THE CORRELATIONS BETWEEN STAGES OF THE ONTOGENY AND THOSE OF PHYLOGENY.

<i>Ontogeny or Development.</i>			<i>Phylogeny or Evolution of the Phylum.</i>		
Structural Conditions.	Stages.		Structural Conditions.	Stages.	Dynamical.
Anaplasia	Embryonic	Embryo or Foetal	Phylanaplasia	Phylenembryonic	Epacme
	Nepionic	Baby		Phylonepionic	
Metaplasia	Neanic	Adolescent	Phylometaplasia	Phyloneanic	Acme
	Ephebic	Adult		Phylephebic	
Paraplasia	Gerontic	Senile	Phyloparaplasia	Phylogerontic	Paracme

The dynamical terms are quoted from Haeckel, and were used by him to designate the phenomena of the rise and decline of types, and also the terms anaplasia and metaplasia. He, however, used 'cataplasia' in place of paraplasia, which is here preferred on account of the faulty derivation of cataplasia.

He realized the importance of these phenomena, and also the significance of the structural characteristics of decline, but did not trace out the distinct correlations which are claimed as fundamentals in bioplastology.

The terms anaplasia, etc., and their correspondents, phylanaplasia, are the structural correlatives of dynamical terms, epacme, etc., and will be found useful when the statical phenomena or structures are mentioned or contrasted with the dynamical phenomena, or with periods of time in which they occur, since the terms epacme, acme, and paracme also refer to time. Terms of the ontogeny are placed opposite to their correlatives in the column of phylogenetic terms, but in reading the table it should be clearly understood that the individual whose life history is represented by the first three columns is supposed to have been taken from the midst of those that lived during the acme of the phylum and belonged to a phylephebic species. In studying the development of such an individual it has repeatedly been observed that the embryo repeated the adult characters of the most ancient representatives of the phylum, which are here called, in accordance with this evidence, phylembryonic.

It has also been ascertained that there are full-grown types in the epacme and acme of groups which correspond to the transient nepionic or baby stage of those that occur later in time; these are the phylonepionic; others have similar correspondences with the neanic stages, and are properly designated as phyloneanic types or forms. The structures of the ephebic (adult) stage are essentially the differentials of the time and fauna in which they occur, and necessarily have no correlations with the past. Their relations are obviously and wholly with the present, except in so far as they represent the consummations of evolution in structures. The structural changes in the gerontic stage of the individual are repeated with sufficient accuracy in the adult, and often even in the neanic stages of types that occur in the paracme of the evolution of a phylum, so that one is forced seriously to consider whether they may not have been inherited from types that occur at the acme of the same group. The fact that these changes occur first in the ontogeny during the gerontic stage does not necessarily imply that they first make their appearance after the reproductive period. No gerontic limit is known to the reproductive time in the lower animals, and it may well be that the continual recurrence of gerontic stages in individuals during the epacme of groups may lead to their finally becoming fixed tendencies of the stock or hereditary in the phylum, and thus established as one of the factors that occasion the retrogression or paracme of groups. The paracme may also be considered as occasioned by changes in the surroundings from favorable, as they must have been up to acmatic time, to unfavorable during the succeeding paracmatic period in evolution. Still a third supposition is also possible, namely, that the type, like the individual, has only a limited

store of vitality, and both must progress and retrogress, complete a cycle and finally die out, in obedience to the same law.

All of these views can be well supported, but, whatever may be the true explanation, it is obvious that there are plenty of paracmatic types, which, in their full-grown and even in their neanic stages, correlate in characters and structures with the characters and structures that one first finds in the transient gerontic stages of acmatic forms of the same type. These can, therefore, be truthfully and accurately described as phylogerontic in the phylum.

In other words, one is able to apply gerontic changes in the ontogeny to the deciphering of the true relations, the arrangement and classification of forms occurring in the paracme, just as Agassiz's law of palingenesis can be used to explain the relations of the links in the chain of being forming the epacme of groups.

The cycle of the ontogeny is, therefore, the individual expression and abbreviated recapitulation of the cycle that occurs in the phylogeny of the same stock; and, while the embryonic, nepionic, and neanic stages give us, in abbreviated shape, the record of the epacme, the gerontic stages give, in a similar manner, the history of the paracme.

The difference between the nature of the two records is, however, necessarily as great as between the beginnings and the endings of existence. The successive stages of the individual are derived from the past, and simply point backwards along the track traversed by the phylum; the changes of the gerontic stage, on the other hand, point to the future, and are prophetic of what is to come in the decline of the type. The retrogressive decline of the individual and that of its type are along parallel lines, and the two are in direct correlation, so that the former becomes an abbreviated index of the latter.

One of the most useful results of these studies has been the method of work developed, the mode of study by series. To follow it out successfully, one must trace the terms of series from the first or most primitive grade to the last, through perhaps long periods of time, and, if upon the same level, through many gradations of structure.

The histologist or embryologist picks out a convenient form here and there for thorough investigation, but does not seem as yet to see the importance of the point of view here insisted upon, viz. that the only method of getting at the correlations of ontogeny and phylogeny is by following out the history of representative series of genetically connected embryos, and the same is true of the experimentalist. While, consequently, their results have been in the highest degree instructive and

progressive along other lines of research, they throw no very strong light on the laws of evolution, and the best modern works on embryology, zoölogy, and experimentation neglect the only proper and efficient mode of studying one very important side of their subject.

One of the results of this mode of study has been the discovery of the law of acceleration in the inheritance of characters, or tachygenesis. Thus it has been found that characteristics are inherited in successive species or forms in a given stock at earlier and earlier stages in the ontogeny of each member of the series. These characteristics, as a rule, disappear from the ontogeny altogether in the terminal, or last occurring, members of a series, and terminal forms thus become very distinct in their development. This law I habitually illustrate as the crawling, walking, hopping, skipping, and jumping law.

Another result of this mode of study is the discovery that, in most genetic series, primitive forms exhibit much greater indifference to geologic changes, persist with comparatively unchanged structures through longer periods of time than those that occur at the acme of groups, and paracmatic forms, if widely distributed, are apt to be particularly short lived, and are very often narrowly localized in origin and duration. Primitive forms are also less changeable in their ontogeny; the adult differs less from either the young or the old than in acmatic forms. The same is true of phylogerontic forms; their old age and youth are less distinct from each other as stages than in acmatic forms. Primitive forms are less affected by gerontic changes in their ontogeny, that is, they have shorter old-age stages, than acmatic forms. Paracmatic forms have much longer old-age or gerontic stages than acmatic forms.

Lastly, it has been found that at the beginning of the evolution of any stock the progress was not only very rapid, but the departures in structures much more marked between the diverging lines of different species, genera, or families, and so on, than those that subsequently occurred in any one of these. This rapidity of expansion is also marvellously sudden in every series near its point of origin, and it is equally so in the whole animal kingdom, which appears with the larger proportion of all its principal divisions in the earliest known fossil-bearing rocks. Each series or type appears to have had a more or less free field, and its first steps in evolution were obviously not affected by natural selection. Subsequently, in the acme of the same series or type, the departures became less marked, and the divergences took place in less important structures; in other words, as stated above, the evolution is slower.

On the other hand, after the acme is passed and the paraecme sets in, there is a sensible quickening of evolution during decline.

Phylogerontic forms become more and more numerous, and there are wider departures in the structures from the acmatic forms than any of the divergences that occur within the acmatic forms themselves.

The hopping, skipping, and at last the jumping, begins in the extremes of the series, so that it becomes difficult, as has been shown by the author in a number of series, and by Cope when giving illustrations of the action of the law of tachygenesis, to connect one of these extreme forms with its nearest congeners.

The characters of the cycle in the ontogeny are here again similar to those of the phylogeny; thus the final substages of the gerontic stage are wider departures from the ephebic substages than these are among themselves and when compared with each other. The analogy of the old with the young shows this most conclusively, and the similarity of phylogerontic and phylonepionic forms in the same stock occurs in the phylogeny.

In fact, there is no end to the homological and analogical similarities and parallelisms of ontogeny and phylogeny wherever both are found complete.

There are types in which the ontogeny is incomplete, as among insects and other purely seasonal animals, and in these it becomes difficult, if not impracticable, to study the gerontic stages, and thus translate the phylogerontic types if they occur. These same types, and others also, present difficulties in their larval stages, owing to their indirect modes of development, which have been discussed by the author in "Insecta" and other publications, and need only be referred to here.

One of the bearings of these researches is of interest on account of the discussions between biologists, geologists, and mathematicians with regard to the length of time that life has existed on this planet, and the bearing of this upon calculations with regard to the age of the earth. It cannot be assumed that the time ratio was the same during the Eozoic or Pre-Paleozoic as during the Paleozoic or the Mesozoic, so far as the evolution of forms is concerned.

The author in other publications has claimed that this must have been the law, and explained the phenomena as parallel with that which takes place at the beginning of every series arising in the Paleozoic and Mesozoic, and also according to Minot's law of growth and other phenomena of the earlier stages in the ontogeny of every animal.

The evidence is very strong that great structural differences were evolved much more quickly in these early times, and the probabilities



are that the progressive steps of the evolution of the primitive types of organisms took place with a rapidity unexampled in later ages. If the laws of bioplastology are true, the evolution of these forms must have occurred more quickly than those of their descendants, except some isolated phylogerontic types and phylopathic forms.\* Man being the most remarkable of these phylogerontic types, we can at once realize what this statement means. If his remains in all their vastness were a part of geological history, and could be contemplated separated from the artificial halo of idealism, it would be seen that they were the direct results of the law of tachygenesis acting upon the basis of a simian organization and exceptional, as compared with other phylogeronts only because of this exceptional basis.

All inferences with reference to the length of time that life has existed upon the earth are consequently defective, since, as far as known to the author, they do not take into consideration this law of variable proportions of time in evolution of organisms at different stages in their history.

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\* The phrase 'evolution by saltation' has been used for the sudden appearance of divergent types by several authors, first by Dr. W. H. Dall; but this seems to me to be simply a mode of expressing a general fact, or series of facts that occur everywhere, and in all series more or less through the action of the law of tachygenesis.